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Predation risk, elk, and aspen: comment

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With the exception of humans, gray wolves (*Canis lupus*) are perhaps the most significant predator of cervids in the northern hemisphere, mainly due to the group-hunting, year-round activity, and widespread geographic distribution (Peterson et al. 2003). Thus, interactions between wolves and large herbivore prey, such as elk (*Cervus elaphus*) and moose (*Alces alces*), have long been of interest to biologists (Peterson 1995, Jędrzejewska et al. 2000, Mech and Boitani 2003). The potential ecological role this apex predator may have, via trophic cascades, has also received attention in recent years by researchers (e.g., Callan et al. 2013, Kuiper et al. 2013, 2014), wildlife management agencies (e.g., state wolf management plans), as well as the general public. Perhaps nowhere in the western United States has a heightened examination of this large predator been more focused than in Yellowstone National Park (YNP; Laundré et al. 2001, Smith et al. 2003, 2013, Fortin et al. 2005). Here, wolves were reintroduced in the mid-1990s, again completing the park's large predator guild after approximately seven decades of absence, thus providing a long-term, landscape-scale, natural experiment (Diamond 1983).

The Gallatin winter range is one of two that occur along the northern portion of YNP, the other is the northern ungulate winter range, or "northern range," located some 25 km or more to the east. Of these, the Gallatin has been less studied. Nevertheless, the Gallatin winter range, like the northern range, experienced high levels of elk herbivory following the extirpation of wolves in the early 1900s. Over a period of approximately seven decades, intensive herbivory by elk led to

the long-term decline in aspen (*Populus tremuloides*) and willow (*Salix* spp.) recruitment (i.e., growth of young plants above the browse level of elk) in the Gallatin winter range, leaving these plant communities in an impoverished condition (Lovaas 1967, Patten 1968, Kay 2001, Ripple and Beschta 2004, Halofsky and Ripple 2008). Accelerated soil and channel erosion also occurred (Lovaas 1967, Beschta and Ripple 2006). Thus, when wolves were reintroduced into Yellowstone in the mid-1990s, aspen recruitment within the Gallatin elk winter range, had been largely absent for several decades (Kay 2001, Halofsky and Ripple 2008).

In 2010, Winnie (2012) sampled 65 aspen stands in the northwestern corner of YNP, within the Gallatin elk winter range, to determine if a behaviorally mediated trophic cascade (BMTc) was occurring. As background information Winnie (2012:2600) included only a single sentence about wolves in the Greater Yellowstone Ecosystem and the remainder of the paragraph briefly discussed elk numbers, with most of the emphasis on elk in YNP's northern range where there has been a pronounced redistribution of elk since the reintroduction of wolves (White et al. 2012). A more complete summary regarding the status and dynamics of wolves and elk over the last 15 years (i.e., 1995–2010) in the Gallatin elk winter range, as well as in the Daly Creek sub-drainage where Winnie's study occurred, would have helped readers better understand the context of his study. Furthermore, information regarding human harvest of elk in the Gallatin winter range since the return of wolves, or whether such hunting has been affecting elk numbers or distribution in recent years was not provided.

As part of his 2010 field study, Winnie (2012) characterized the presence or absence of several hypothesized risk factors (independent variables) for each aspen stand, including escape impediments, visual impediments, distance to conifer forest edge, and presence of deadfall trees. For dependent variables, Winnie (2012) recorded the presence or absence of browsing on aspen suckers (ramets <2 m in height) and the number of aspen juveniles (plants >2 m in height but <6 cm in diameter at breast height). A height of 2 m generally represents the upper browse level of elk, and young aspen exceeding this height are considered to have successfully recruited. Such recruitment would represent a major departure from the browsing suppression that occurred in his study area over recent decades (Kay 2001, Halofsky and Ripple 2008) and an indication that a tri-trophic cascade involving wolves, elk, and aspen may be underway.

From the results of his analyses, Winnie (2012:2600) concluded that "aspen were not responding to hypoth-

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esized fine-scale risk factors in ways consistent with the current BMTC hypothesis.” We respectfully submit that the design and analysis used to support such a conclusion may be deficient for two reasons, the first based on conceptual concerns and the second on statistical concerns. (1) Unfortunately, some aspen stands Winnie (2012) sampled contained juveniles associated with “physical barriers,” barriers that could prevent elk from browsing young aspen. To be scientifically valid, a risk assessment using young aspen as the dependent variable must inherently assure that all evaluated plants were accessible to elk browsing. (2) The inclusion of 10 aspen stands containing some physically protected aspen likely confounded results from his predation risk analyses (i.e., Figs. 5, 6, and 7 in Winnie 2012). While the inclusion of stands with protected aspen may increase the variance associated with his dependent variables (i.e., browsing rate, number of juveniles), the fallacy of doing so is revealed by inspecting these variables for the 85% of his stands ($n = 55$ stands) that did not have physically protected aspen. Here, a browsing rate of $\sim 99\%$ and an average of <1 juvenile per stand occurred (back-transformed means from Fig. 8b and a, respectively [Winnie 2012:2609]), indicating a general lack of variance in the dependent variables associated with these stands and little likelihood of a statistically significant outcome. Thus, we suspect that the “statistically significant” results Winnie (2012) found in Figs. 5, 6, and 7, whether contrary to or in support of a BMTC hypothesis, are primarily influenced by the occurrence of risk factors associated with those stands where some of the young aspen were physically protected. A reanalysis by Winnie of browsing rate and number of juveniles vs. his risk factors, using just the 55 stands accessible to elk, could clarify this issue.

Because of the above concerns, we would offer that results of Winnie’s (2012) analyses of “proportion of sprouts browsed” or “number of juveniles per stand” relative to his hypothesized risk factors may well be spurious. If so, any discussions and conclusions based on those results are in question.

A 2004 field study of aspen stands in the Gallatin winter range found aspen recruitment had declined precipitously following the extirpation of wolves in the 1920s and remained essentially absent through the late 1990s (Halofsky and Ripple 2008). Thus, when Winnie (2012) undertook his field study in 2010, a wolf–elk–aspen trophic cascade had not yet been confirmed. While the occurrence of juvenile aspen would be important to the long-term survival of aspen stands, the data for elk-accessible stands continue to show exceptionally high browse rates and little or no recruitment (Winnie 2012). This situation contrasts with YNP’s northern range where decreased browsing and increased heights of young aspen in portions of that range have been

observed some 6–10 years after the occurrence of increased willow growth, although this recruitment has been spatially patchy (e.g., Ripple and Beschta 2012, Painter 2013; also see northern range photos of aspen recruitment *available online*).⁵ It should be noted that decreased browsing and increased heights of willows in the Gallatin winter range (at the base of the Daly Creek watershed) following the return of wolves, and consistent with the occurrence of a trophic cascade, were documented as early as 1999–2000 (Ripple and Beschta 2004), with heights continuing to increase in more recent years (Beschta and Ripple 2010). Also consistent with a trophic cascade, various northern range studies have found increased willow growth/canopy cover, sometimes interacting with climatic fluctuations, following wolf reintroduction (e.g., Groshong 2004, Beschta and Ripple 2007, Beyer et al. 2007, Baril 2009, Tercek et al. 2010, Marshall 2012).

The occurrence of 192 juvenile aspen within Winnie’s (2012) study area would seem to indicate the beginnings of a tri-trophic cascade, particularly when compared to the lack of juvenile production in the decades immediately before wolf reintroduction (Halofsky and Ripple 2008). However, most of the 192 juveniles were associated with aspen stands characterized as having some degree of physical protection from elk (Fig. 8a in Winnie 2012), making it difficult to confirm if they represent a wolf–elk–aspen trophic cascade involving density and/or behavioral mediation. A trophic cascade involving aspen can be complex and context dependent (e.g., linked to bottom-up factors such as fire [Eisenberg et al. 2013]). Furthermore, undertaking risk assessments associated with large mammalian predators and ungulates in mountainous terrain, where human hunting is also occurring across part of the landscape, can be especially challenging. While we commend Winnie (2012) for attempting such an assessment, without a reanalysis of only those young aspen accessible to elk it would appear that his evaluation may not have been sufficiently rigorous to evaluate the presence or absence of a potential BMTC in the Gallatin winter range.

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⁵ <http://hdl.handle.net/1957/20842>

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Predation risk, elk, and aspen: reply

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The behaviorally mediated trophic cascade (BMTC) hypothesis predicts that fine scale variation in predation risk causes differences in herbivore browsing pressure on woody plants. If the hypothesis is correct, elk browsing pressure on aspen should be low, and aspen recruitment should be high, in places of purported high wolf predation risk in Yellowstone National Park. Using Ripple and Beschta's (2003, 2004, 2006) and Halofsky and Ripple's (2008a) definitions of four risk factors, I tested the ability of purported risk to predict browsing and recruitment of aspen in the Daly Creek drainage in Yellowstone. All of the ingredients necessary to test the BMTC hypothesis are present in the drainage: wolves, elk, purported risk factors, and aspen. The results of my analyses were clear. While purported risk (independent variables) varied from place to place, aspen recruitment did not vary in ways consistent with the BMTC hypothesis. In addition, regardless of purported risk levels, elk had browsed most of the accessible aspen in

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